MATE CHOICE IN FEMALE JAPANESE MONKEYS(Dissertation_全文)

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学位申請論文

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主論文 1.

Behavioral Patterns of Mate Selection and Partner Preferences in Female Japanese Macaques

Running title: Mate selection and partner preferences

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Abstract

Sexual behavior of the provisioned, free-ranging Arashiyama B troop of Japanese macaques (Macaca fuscata) in Japan was studied over three mating seasons between 1979 and 1985. The behavioral patterns of female mate selection were analyzed. Regardless of whether females were alone or with their current consort partner, they demonstrated strong preference for that male by rejecting the sexual solicitations (courtship displays, mount attempts) of others. When put in the situation of choosing between two males simultaneously, females most frequently chose to remain with their consort instead of joining the more dominant intruder male. These behaviors were found to be ineffective in influencing female mate choice. During any given estrous period, the female's first consort partner was associated with the longest in 76-84% of the estrus periods analyzed in all three mating seasons. This tendency suggests that a female's mate choice often occurs before coming into estrus and remains stable throughout the estrous period or mating season. In the 1984-85 mating season, significantly more females had young high ranking male consort partners and significantly more females rejected the older high ranking males. The reoccurrence of consorts over two consecutive years between the same pair was high, but females tended to reject the frequent sexual solicitations of males with whom they had been in consort at least 4-5 years earlier. Instead, these females were selecting to mate with the younger adult males that were not yet sexually active 4-5 years ago. These trends in female partner preference are believed to play an integral role in troop social dynamics and are discussed in terms of the emigration and

immigration of non-natal males.

Key Words:Macaca fuscata, sexual solicitation, mate selection, partner preference, consort formation.

Introduction

Early primate studies emphasized male dominance as a factor in mate selection and mating success. Cox & LeBoeuf (1977) have suggested that due to the controversial nature of female mate choice and, the fact that male behaviors are easier to see, and thus seem of more significance to investigate, females have received less attention. In primates the favored hypothesis places much importance on male dominance for access to estrus females (Carpenter, 1942; Altmann, 1962; Hall & DeVore, 1965). That is, dominant males, by being spatially located in the center of the troop, are able to maintain a priority of access to estrous females (Fedigan, 1983).

More recent studies based on correlations between male dominance and mating frequency suggest that consort interference by males, influence females to prefer high ranking males; preference always being inferred from mating frequency (Hausfater, 1975, Stephenson, 1975; Chapais, 1983). Such reasoning assumes that females play no significant role in the selection of mates and that mate preference is only a matter of degree, i.e. that a female mates more with some males than others. However, other studies have shown that the relationship between male rank and mating frequency is not always clear (Loy, 1971; Sugiyama, 1971; Eaton, 1974; 1978; Enomoto, 1974; Takahata, 1982a), and male dominance has been shown to have no effect on a female's immediate

choice of mates in relation to consort intrusion (Huffman, 1987).

Both Eaton (1978) and Fedigan (1982) have pointed out the difficulties of determining who is initially responsible for the initiation of a given consort i.e., a subtle message sent hours or even several days earlier, may have an affect on consort formation. However, it is possible to show what roles males and females play in the immediate initiation and maintenance of such relationships.

Recent studies of female proceptivity in non-human primates, have described females as playing an active, and sometimes predominant role, in the initiation of mating activity (Taub, 1980; Tsingalia & Rowell, 1984; McDonald, 1985; Harding & Olson, 1986). In addition, females have been observed to exercise one's choice of mates by rejecting the mount attempts of certain males (Enomoto, 1974; Niemeyer & Chamove, 1983; Yamagiwa, 1985; Smuts, 1985 Keedy, 1986,). Most of these reports, however, did not analyze in detail these behaviors and the actual role they played in maintaining partner preferences.

By rejecting or accepting males as mates (mate selection), females are here considered to be exhibiting their preference for particular males over others (partner preference). The preferred attributes which have previously been suggested are; relationships, such as rank (eg. Lindburg, 1971; Hausfater, 1975; Seyfarth, 1978a,b) and previous friendly relationships (eg. Scott, 1978; Packer, 1979a,b; Smuts, 1985), or individual differences and personality traits such as non-aggressiveness (eg. Eaton, 1974; Michael, et al., 1978), aggressiveness (eg. Enomoto, 1981; Modhal & Eaton, 1977), and male novelty (eg. Packer, 1979 a,b; Huffman,

1981; Wolfe, 1984). While these studies recognized the significance of female mate selection and described possible female partner preferences, few directly analyzed the social interactions involved.

In order to better understand the roles and effects of female mate selection, we must know how, and to what extent they effectively maintain partner preferences. The purpose of this study was to investigate the female's role in choosing mating partners, by analyzing the behaviors involved in selecting mates and the resultant trends in partner preference.

Materials and Methods

Subjects

Observations were conducted on the free-ranging, provisioned Arashiyama B troop outside of Kyoto, Japan, during three mating seasons; 1979-80 (October 27 - March 3), 1983-84 (November 13 - February 21) and 1984-85 (September 29 - March 4). From here on, these three mating seasons will be referred to as study periods I, II, and III, respectively. During this study the troop consisted of 263 individuals (including 35 adult males 4.5 + years: 111 adult females 3.5 + years) in 1979, 236 individuals (27:89) in 1983 and 250 (41:99) in 1984. The decline in population between study periods I and II was due mainly to systematic capturing by the park management. Adult males and females were classified by age into the following categories: Males (subadult 4.5-9.5, adult 10.5 + years); Females (pubescent 3.5-6.5, middle age 7.5-16.5, old age 17.5 + years)(after Takahata, 1980). This paper is based mainly on the data from the latter two study periods.

Observations

Sampling procedures varied over the three study periods. During the first study period observations were carried out by sampling all observed occurrences of sexual behavior. In the second study period, all observed occurrences of some behaviors, sequence sampling and ad lib. sampling methods were used (Altmann 1974). During the third study period focal animal sampling was conducted on all females observed to be in estrus on a given day (at least twice that day when possible) and sequence sampling of some behaviors. For sequence sampling of courstship displays, the female was observed for at least 5 minutes after the male's approach or until the end of a mounting-series if one occured between them.

Each focal sample was 15 minutes in duration or longer as determined by the end of a consort intrusion event or mounting-series (See Huffman, 1987 for details). In all three study periods the menstrual states (i.e. vaginal bleeding, seminal plug, absence or presence of sexual swelling, facial coloration) of all females observed in and around the feeding station area were recorded daily, and their mating activity followed. The observed mounting-series of all troop members were recorded (ad libitum). Additional mounting-series recorded by other observers in study period III were combined with the author's observations for general descriptive purposes only.

Statistical Analysis

Throughout the analysis simple descriptive statistics were used to describe the general structure of observed behaviors. In testing the immediate outcome of a female's response to all male solicitation behaviors (Table 2), Fisher's exact probability test

was utilized instead of x^2 test of independence because an expected frequency of less than 5 in one (less than 80% of total cells) of the cells occurred. The Spearman rank order correlation (r_s) was used when testing for correlation between age / rank and other variables.

Dominance Rank

Female rank order was determined from the distribution of submissive behaviors during both non-feeding and feeding situations in the 1985 non-mating season. The matrilineal rank order of the troop remained basically the same as that reported by Takahata (1980), and, therefore, was used in all three study periods. Male rank order was determined by the distribution of submissive behavior among them; except for some males seldom or never observed together. These males are listed by age and lineage rank after Koyama (1967). These males (4.5+ yrs.) could be divided into two groups; high and low ranking, as classified by their socio-spatial position in the troop during the non-mating seasons. High ranking males were those adult males found in the central area of the troop in and around the feeding station area. The low ranking male group included all adult and subadult males found only in the peripheral area of the troop during the day time. Included in this group were, visiting non-troop males, seen during the mating season in the peripheral areas of the troop during the day.

In study period I there were 6 high ranking males and 12 low ranking males observed mating, in study periods II and III, there were 5 high-9 low and 6 high-19 low ranking males respectively, observed mating. Also, the mounting-series of four immature

males, Gl-6482♂, Op-6082♂, Op-60657382♂ and Mi-63697481♂, two and three year old males, were included in the analysis of some behaviors (Figures 2, 3) as they were actively sought as partners.

Definition of terms

Estrous period: The period in which the female is in estrus (see Carpenter, 1942; Takahata, 1980; Huffman, 1987 for details of estrus and related behaviors). A duration of 9 days or more between the cessation of sexual activity and its resumption was arbitrarily used to distinguish and differentiate between two estrus periods. Consort: The sexual association between a male and female which includes the frequent synchronization of feeding, resting and traveling. The consort lasts from one mounting-series up to several days (multi-day consort) over one estrous period. Multi-day consorts were sometimes disrupted by days in which the pair were not observed mating. Figure 1 shows the distribution of the duration, in days, in which mating was not observed between multi-day consort pairs and the frequency in which the female mated with other males during a duration of X days. Over a duration of more than 3 days, the female became increasingly more likely to mate with other males. Thus, multi-day consort pairs can be operationally defined as temporarily out of consort, if they are not observed mating for more than three days. Male sexual solicitation: Behaviors directed toward estrous females signaling a male's motivation to mate by attempting to; gain proximity to the female and establish or maintain a mounting-series (Stephenson, 1973). See Enomoto, 1974 and Rostal & Eaton, 1983 for general description of representative behaviors.

Results

Patterns of Female Mating Behavior

Consort Partners and the Estrus Period

Females were observed in estrus 1-4 times (x= 1.92, S.D.= 0.93, n= 156, 3 mating seasons) during the mating season, with each estrus period lasting a mean of 8.9 (S.D.= 8.4) days, with a range of 1-42 days. The few females with long estrous periods, tended to spend most of that time with one particular male. Duration of the estrous period varied considerably among females, and in the same female over the mating season.

During any given estrous period, females were observed to have had 1-9 different mating partners (x= 2.32, S.D.= 1.54, n= 156). The total number of males associated with over the entire mating season was 1-10 (x= 3.8 S.D.= 2.06).

Duration of the consort

From all three study periods, a total of 369 consorts among 302 pairs, were analyzed with respect to continuity of the consort during an estrous period. During an estrous period, the majority of consorts were observed to end within one day (single day consort). They accounted for 72% (n=58/81), 72% (n= 34/47) and 65% (n= 156/241) of the consorts followed during an estrus period in the I, II, and III. study periods, respectively. The remaining 28-35% of the these consorts, continued over a period of 2-38 days (x= 6.89, S.D.= 5.34, n= 121) during a given estrous period and are referred to here as multi-day consorts. While such pairs did not always spend this entire period together, some continued in consort for almost the entire estrous period. In study period III they were observed consorting from 1-7

consecutive days (x= 1.64 S.D.= 1.13, n= 165 among 85 pairs), temporarily splitting up for 1-12 days before rejoining. It was usually the male that would discontinue the consort when his attentions would be drawn to another female. During these periods females briefly consorted with other males, or did not mate at all (figure 1).

While these consorts were observed much less frequently than single day consorts, of all the females whose sexual activity was monitored during the three study periods, 61% (I. n= 14/23), 64% (II. n= 11/17), and 69% (III. n= 31/45) had at least one multi-day consort. In all three study periods combined, 82% of these females had one or two different long-term consort partners.

Pattern of multi-day consort formation

Frequently multi-day consorts started at the beginning of a female's estrous period. In all three study periods most often the females spent the greatest number of days in consort with the first consort partner of the estrous period. In all three study periods this pattern was recognized in 84% (21/25), 80% (12/15), and 76% (38/50) of the estrus periods analyzed.

Mate Selection

Male sexual solicitation and female mate selection

Estrous females often were observed to be approached by males. Females avoided most of them by moving away, approaching and interacting only with certain males. Three types of courtship were analyzed for patterns of female mate selection and trends in mate preference. These behaviors could be divided into two situations, those directed towards: 1) lone estrous females, and 2) estrous females engaged in mating activity with other males.

1 Behaviors directed toward lone estrous females

During study period III, a total of 94 courtship displays were observed among 74 pairs, by behavioral sequence sampling (see methods above). The interaction was initiated by the male chasing after the female (51%), walking towards her (37%), or by suddenly attacking without warning (11%). In 77% (n= 72) of these solicitations the pair separated within 5 minutes and no further immediate interactions occurred. The male most often (n= 47) left shortly after solicitating if the female showed no favorable response (female leaves n= 17, both move away n=8). Once a male unsuccessfully attempted to forcefully mount the female. In the remaining 23%, the pair temporarily remained together. Both male and female were found to take the initiative in maintaining proximity by following the other or initiating grooming. A mounting-series resulted in only 2 of these events.

Courtship displays among pairs that had not been observed to mate previously may affect the females future choice of partners. Consorts were recognized between 31% (n= 23/74) of all males and females observed in these interactions. However, only 8 were observed to begin sometime after courtship display was first observed; 7 of these consorts did not start until the next estrous period.

Another form of mounting-series initiation for a male, if he has gained proximity to a female, is to prompt her to stand for mounting by placing his hands on her hips. During study period III, 89 focal observation sessions among 33 pairs were observed in which the female avoided (n= 215) a male's attempts to initiate a mounting-series. The most frequent response was for the female

simply to refuse to stand (55%) or to stand while keeping her hindquarters lowered (27%). If the male attempted to mount while the female was standing, she most often just lowered her hindquarters or moved away (18%).

In 82% (73/89) of all sessions, among these 33 pairs, avoidance was complete. Regardless of the male's persistent attempts (1-10 times per session) to initiate a mounting-series, the females had control of the interaction. In four of these sessions the male ejaculated on the female's back never having gained intromission. In the remaining 18% (n= 16/89) of these sessions, the male was currently (n=13) or had previously been (n=1) in consort with the female. He was refused (1-2 times) sometime during an otherwise normal mounting-series; 14 of which ended in intravaginal ejaculation.

2 Behaviors directed toward estrous females with another male.

During study periods II and III, 343 consort intrusions were observed. The intruder was dominant over the male of the intruded upon pair except in 9 cases. Intrusions were directed mainly towards the female and closely resembled the courtship display behaviors directed toward lone estrous females, as described above. These behaviors were also found in courtship behavior observed between stable consort pairs.

In 77% (264/343) of these intrusions, the intruder male was unable to prevent the pair from continuing their association (Table 1). Notably, in 63% (166/264) of these cases, it was the female who took the initiative of continuing the association by reapproaching her partner. In only 2% (7/343) of all observed intrusions, did a mounting-series between the intruder male and

female start immediately afterwards during the same observation session. In all 7 cases it was the female who initiated the mounting-series. All but one of these pairs were currently in a multi-day consort.

Using only the data set from study period III (293 cases, among 151 intruder male-female pairs), for which observations were most complete, mating was not observed among 64% of these pairs. Among pairs recognized to have had been in a multi-day consort (n=40) before or during the same period as the male intruded upon the female, the interaction resulted in mating in only 3 (2 pairs) out of 54 cases. Females were more likely to continue the present mounting series than start a new one with the intruder male, regardless of whether or not he was or had previously been a consort that mating season. Consorts were recognized to begin for the first time that mating season after intrusion was first observed in only 14% (n= 21/151) of the intruder male-female pairs.

The above three types of male sexual solicitation behaviors may have some effect on a female's future mating partner choice, but because of the delay between their occurrences it is difficult to evaluate their effectiveness. Combining the possible effects of all three behaviors by given males during study period III, only 16 pairs (7%) were observed to begin their first consort later on that mating season.

Mating Partner Preferences

Preferential mating

A strong preference for the current consort partner over

another male was shown by the females' response to the latter's sexual solicitations during the period of her consort with the former. The first three of the following four analyses were carried out on the 31 females in one or more multi-day consorts in study period III (Figure 2 and 3). Each of these females mated with 1-7 males (x= 3.44, S.D.= 1.70) while actively rejecting the sexual solicitations of another 1-5 males (x= 2.34, S.D.= 1.54). Females rejected 43% (80/188 pairs) of the males observed to solicit mating with them.

1 Current sexual relationship with the male

Females responded differently to male sexual solicitation with respect to whether or not that male was currently in a multi-day consort with her. These results are summarized in Table 2. Mounting-series followed male sexual solicitation significantly more often if the soliciting male was currently in a multi-day consort with the female ($p < 0.001$, Fisher's Exact Probability Test).

2 Female age and rank

Relatively older more experienced females tended to have had more mating partners (Figure 2). ($r_s= 0.39$, $p< 0.05$, n= 31 females). However, no significant correlations were recognized in a female's age and the number of males rejected or a female's rank, and number of males mated with or rejected ($r_s= 0.15$, n= 28 rejecting females; 0.22, n= 31 all females; 0.14, n= 28).

3 Male age and rank

The same males were associated with differently by each female encountered i.e., individual variation in female mating partner preference occurred (Figure 3). However, trends with respect to

the age and rank of males were found. More females tended to have had relatively older subadult and adult, high ranking mating partners (r_s= 0.41: age, $p < 0.05$: rank , n= 22 males, age of two males unknown; r_s= 0.61, $p< 0.001$, n= 24). (Among all subadult and adult males, age was significantly correlated with rank (r_s= 0.80, $p < 0.001$, n= 19)). Looking at the 6 highest ranking adult males, found in the central part of the troop, these trends were reversed. More females tended to have had more lower ranking partners (r_s= 0.87, $p< 0.05$, n= 6 males).

With respect to the rejection of solicitations, more females rejected those of higher ranking adult males (r_s= 0.93: rank; 0.80: age, $p < 0.001$, n= 22 males). More females rejected the solicitations of higher ranking males, in particular the first and second ranking males (r_s= 0.94, $p< 0.05$, n= 6).

4 Mount attempt refusal and mating frequency

Looking at mount attempt refusals only (Figures 4), refusal was limited to the seven highest ranking adult males. In particular the first, second, and third ranking males accounted for 52%, 26%, and 16% respectively, of all (n=262) observed events in study period III. If the chances of having ones mount attempts refused is related only to the frequency of mounting series it can be predicted that males who mate more often should be refused more often. This prediction was not fulfilled (r_s= 0.38, n= 6).

Sexual familiarity and long term trends in mating partner preference

Of 30 pairs (19 females) observed mating in study period II, in which males and females were present and sexually active the next year, 73% were recognized in consort again in study period

III. Out of 11 mating pairs (9 females including 2 from above) observed in study period I, for which males and females were present and sexually active in both of the following study periods, only 2 pairs were observed in consort four years later in period II, and only one of these pairs consorted again in period III.

Among the remaining 10 pairs not observed in consort during the latter two study periods, females of 7 of these pairs rejected the frequent sexual solicitations of the male. Instead, these females mated with males not yet sexually active during periods I or II (n= 24 pairs), or with other adult males, not observed in consort with her during these two periods (n= 2 pairs).

Discussion and Conclusions

This study was concerned with the analysis of behavioral patterns of female mate selection behavior and partner preference. Females had the decision as to whether or not mating occurred. Females displayed clear preference for given males by actively initiating and maintaining multi-day consorts with them and by rejecting the solicitations of other males during this period. This view is in accord with previous reports on Japanese macaques (Enomoto, 1974; Takahata, 1982a; McDonald, 1985) and demonstrates the key role females play in mate selection.

A female's mate choice appears to occur often before coming into estrus and was shown to be affected by the amount of previous sexual relations with potential partners rather than the immediate effects of solicitation itself. In this sense, male sexual solicitation behaviors can be viewed as perhaps playing a larger role in synchronizing the behavior and level of arousal between

two individuals leading up to copulation rather than directly influencing the selection of mating partners, as current sexual selection theory suggests.

Individual variation of possible preferred male traits was recognized i. e,. the same male was sought after by certain females while consistently avoided by others. This is consistent with the observation that females tended to avoid mating with those males whom they were sexually active with at least 4-5 years earlier. This diachronic view of mating partner preference raises doubts about the selectability of dominance rank as a discrete male attribute by females. Among macaques it has been shown that male rank is correlated with age, as is male tenure (Hanby et al., 1971; Rowell, 1974; Drickamer & Vessey, 1973; Norikoshi & Koyama, 1975). Among this group of primates it becomes particularly hard to differentiate between possible preference for age, rank, or tenure. However, in this study it was suggested that a male's age or tenure, was of greater importance than rank.

In Japanese macaques and rhesus, it has been proposed that special affinitive relations which develop between adult male-female pairs through sexual relations frequently lead to the avoidance of mating between them after the first two or more years (Takahata, 1982a,b; Chapais, 1983). It is proposed here that the formation and maintenance of non-sexual relations after sexual ones is largely the result of female mate choice. Smuts (1985) argues that intimate relations or "friendships" in olive baboons promote rather than inhibit sexual relations between "friends". However, her study on the consort relations of such pairs lasted only two years and she presents no data on the further development

of sexual relations between "friendships" that persisted for more than five years i.e., cases in which these males remained in the troop for several years. Such information would be useful in better understanding the similarities and differences between these species with regards to female mating preferences. In this study, while data is not presented about the status of intimate proximate relations which may have developed between consort pairs, similar trends as those described by Takahata and Chapais, were recognized here in mating avoidance for pairs observed in prior long term mating relations and provide interesting comparison.

The patterns of mate selection and partner preference over time as described here suggests that female mate choice may be an important catalyzer to the Japanese macaque mating system. The tendency for estrous females to show interest in sexually unfamiliar males appears to be a widespread phenomenon and has been shown to be helpful in the acceptance of these males into the troop social hierarchy (i. e., Fukuda et al. 1974; Packer, 1979; Henzi & Lucas, 1980; Collins, 1981; Smuts, 1985). In rhesus and Japanese macaques, the increase in female support for younger males (increase in reproductive- / mating- success) has been observed to precede changes in male rank (Smith, 1981; see Huffman, 1987; Huffman, in press for an example).

Norikoshi (1976) has suggested that a decline in the number of mating partners, may be partly responsible for the emigration of non-natal troop males. Between 1981 and 1987 the successive emigration of two alpha males, Ma-59♂ and K-63♂ was recognized (Huffman, in press). In both cases, inspection of previously

published data revealed a gradual decline in mounting-series frequency during their tenure as leader class central troop males (Stephenson, 1975; Takahata, 1982a; Huffman, 1981; 1987). While both males were active consort solicitors, the decline in mounting series toward the end of each male's respective tenure was largely due to female avoidance of their consort initiation attempts. Similar observations have been made for 3 alpha males and 2 fourth ranking males among the A, B, and C troops at Takasakiyama. Their gradual decline in mating activity and an increase in female rejection was accompanied by the increase of consorts with neighboring troop females. With the exception of one male who disappeared completely from the area, all the others transferred into the troop of their consorts (T. Matsui, unpublished data).

In Japanese macaques, adult males in small sized troops (15-60 indiv.) tend to leave after 2-4 years in the troop; most frequently during the mating season (Sugiyama & Ohsawa, 1974; Fukuda et al. 1974, Suzuki et al. 1975; Yamagiwa, 1985). The recorded Arashiyama troops have been relatively large sized and isolated. These two factors probably effect the degree to which female mate choice influences male tenure. Being relatively isolated from other troops, the opportunities for transfer are less frequent and as they must travel over long distances (15-30 km; Hieizan, Minoo troops: see Huffman, in press). Thus, males which have acquired stable social positions within the troop may stay longer than others. With an increase in troop size we can expect an increase in the number of adult females with which to mate, making it easier for these males to stay in the troop for a longer period of time. At Arashiyama between 1960 and 1981 there

were 5 non-natal males (Arashiyama troop and B troop) recognized to reach alpha status before leaving the troop. During this period, the troop grew in size from 62 to over 236, and the length of tenure of these non-natal males in the central part of the troop (range 15-179 months, mean=71) increased accordingly (Huffman, in press). The correlation between length of male tenure and average troop size is statistically significant (r_s= 0.96, n= 5, $0.05 > p > 0.01$).

Taking into consideration troop size and the frequency of inter-troop interaction, the above discussion suggests that in the society of Japanese macaques, female mate choice and partner preference plays an important role in troop social dynamics. Further detailed observations are needed in order to better understand how a female's mate choice is made and how the consort begins. Itani (1972) has pointed out that the emigration of adult non-natal Japanese macaque males after 3-4 years in the troop, the time at which his possibly first born female offspring matures, results in the avoidance of possible inbreeding (father-daughter incest). This can be said for most primate species in which males migrate out (eg. Henzi & Lucas, 1980). The behavioral mechanisms of female mate selection and partner preference may be considered to be one of the important factors influencing incest avoidance. The influence of female mate choice, on proposed male mating strategies has received little attention and should prove to be a fruitful area of research in the future; adding to a more balanced understanding of primate mating systems and their evolution.

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Table 1. The immediate outcome of consort intrusion. Data combined from 1983-84 and 1984-85 mating seasons (N= 343).

Association continues	Events	(%)
Male reapproaches	14	
Female reapproaches	63	
Pair reunite in new location	14	
Pair not separated by intrusion	9	
		n= 264
Association temporarily terminated		
Pair separate, intruder leaves	34	
Intruder approaches remaining near female, partner leaves	23	
Female initiates mounting-series with intruder	9	
Female approaches new male, intruder and previous partner leave	10	
Outcome unknown	24	
		n= 79

Table 2. Outcome of male sexual solicitation towards estrus females with respect to whether or not the pair were currently in multi-day consort (N= 289).

	not in consort		in consort		sub-total
	mounting-series starts				
When female is alone	yes	no	yes	no	
Courtship display (events)	0	56	2	0	58
Mount attempt refusals (sessions)	3*	58	13	4	78
When female is with consort another partner					
Consort intrusion (events)	1*	137	3	10	151
total	4	251	18	14	

* The male was previously a consort partner sometime that mating season.

Legend to figures.

Figure 1. Distribution of the frequency of the duration in days in which mating was not observed between multi-day consort pairs and the frequency of the duration in days after which the female was observed mating with other males.

Figure 2. Individual differences in female mating patterns in the 1984-85 mating season, with respect to the number of consort male partners and rejected solicitors. This figure includes only those females observed in at least one multi-day consort. Females are listed in rank order. The last two digits of the name indicate year of birth.

Figure 3. Individual differences in male mating patterns in the 1984-85 mating season, with respect to the number of female partners consorted with and rejected by. This figure includes only those associations between these males and the 31 females observed in at least one multi-day consort. Males are listed in rank order. The last two digits of the name indicate year of birth.

Figure 4. Frequency of mount attempt refusals recieved versus total mounting series frequency during the 1984-85 mating season. This figure includes all mount attempt refusals observed this season.

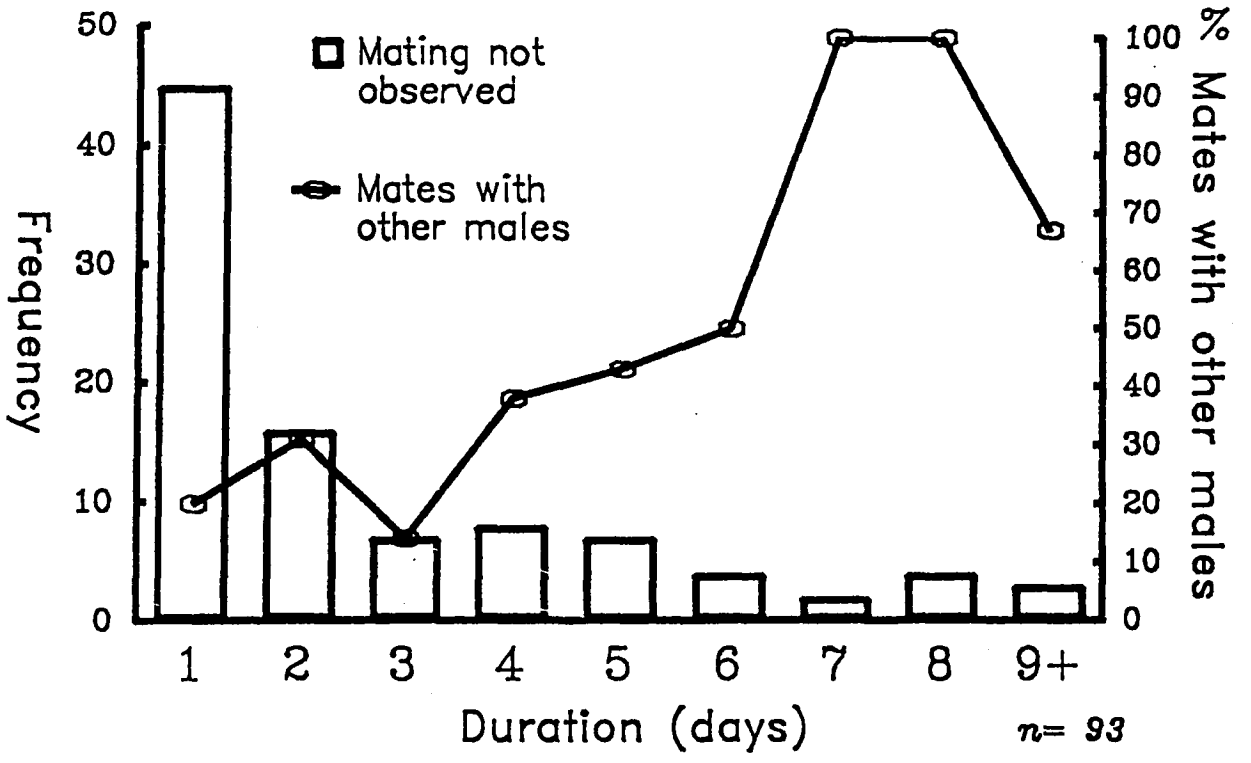
Mating not observed
Mates with other males
Frequency
% Mates with other males
Duration (days)
n= 93
0
10
20
30
40
50
60
70
80
90
100
1
2
3
4
5
6
7
8
9+

Fig. 1

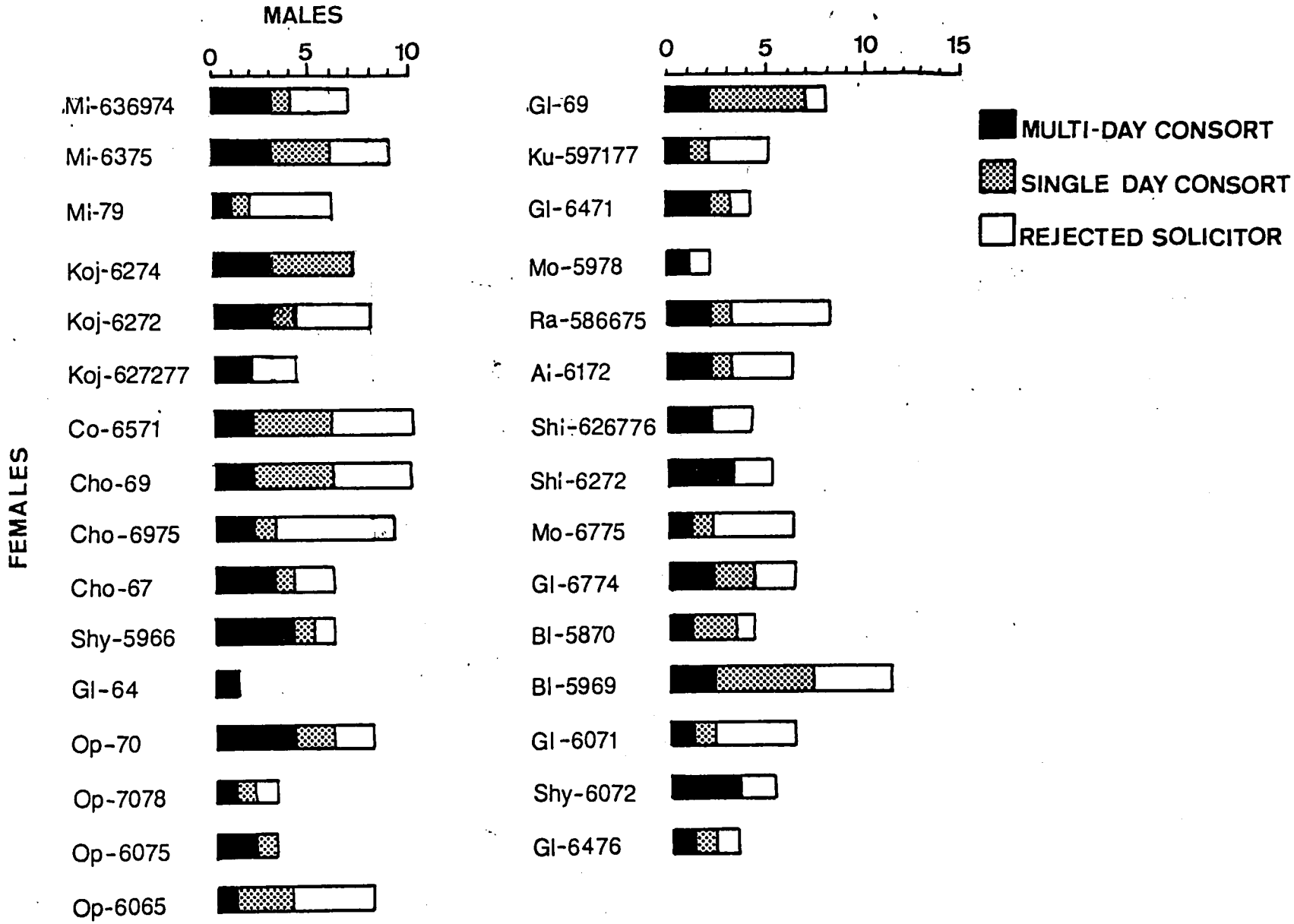
MALES
0
5
10
15
FEMALES
Mi-636974
Mi-6375
Mi-79
Koj-6274
Koj-6272
Koj-627277
Co-6571
Cho-69
Cho-6975
Cho-67
Shy-5966
Gl-64
Op-70
Op-7078
Op-6075
Op-6065
Gl-69
Ku-597177
Gl-6471
Mo-5978
Ra-586675
Ai-6172
Shi-626776
Shi-6272
Mo-6775
Gl-6774
Bl-5870
Bl-5969
Gl-6071
Shy-6072
Gl-6476
MULTI-DAY CONSORT
SINGLE DAY CONSORT
REJECTED SOLICITOR

Fig. 2

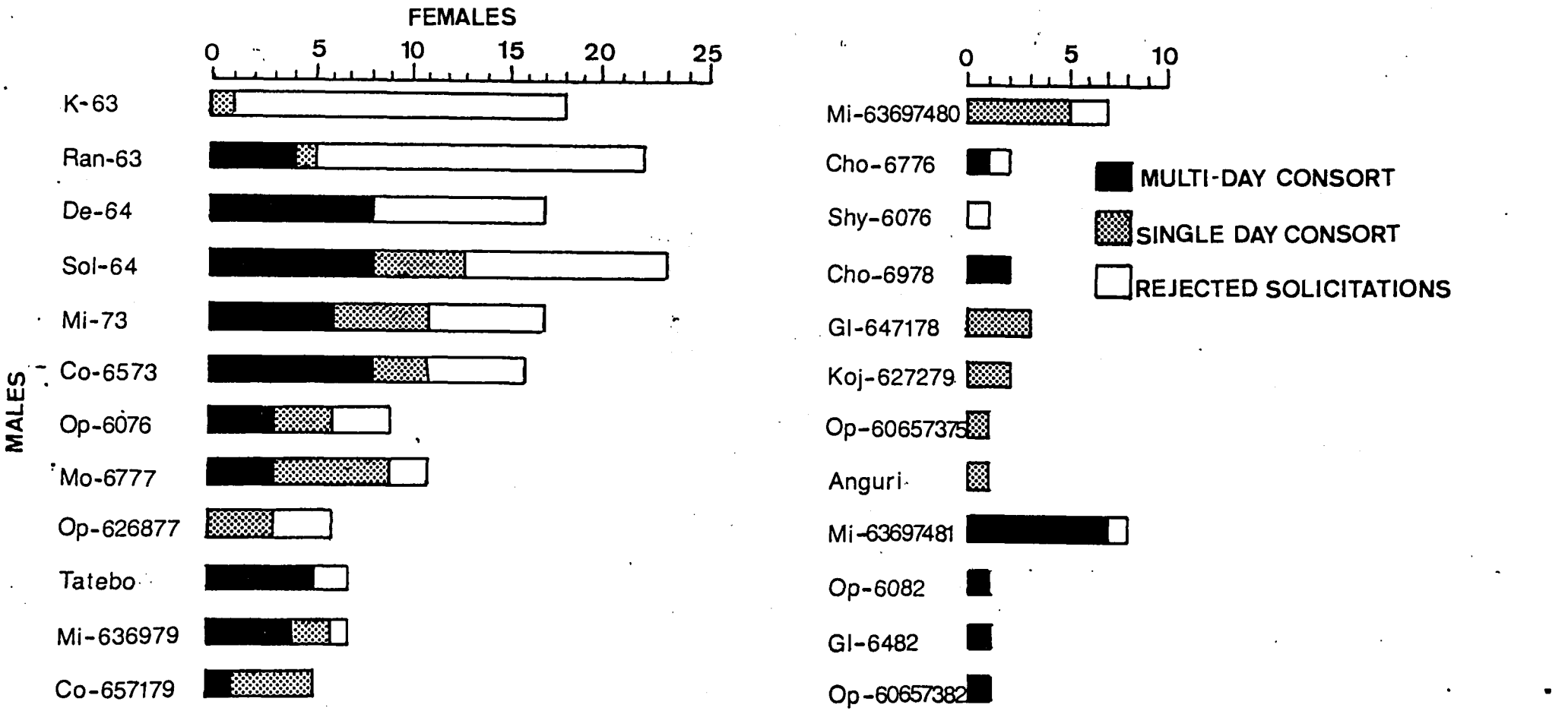
FEMALES
0
5
10
15
20
25
MALES
K-63
Ran-63
De-64
Sol-64
Mi-73
Co-6573
Op-6076
Mo-6777
Op-626877
Tatebo
Mi-636979
Co-657179
0
5
10
Mi-63697480
Cho-6776
Shy-6076
Cho-6978
GI-647178
Koj-627279
Op-60657375
Anguri
Mi-63697481
Op-6082
GI-6482
Op-60657382
MULTI-DAY CONSORT
SINGLE DAY CONSORT
REJECTED SOLICITATIONS

Fig. 3

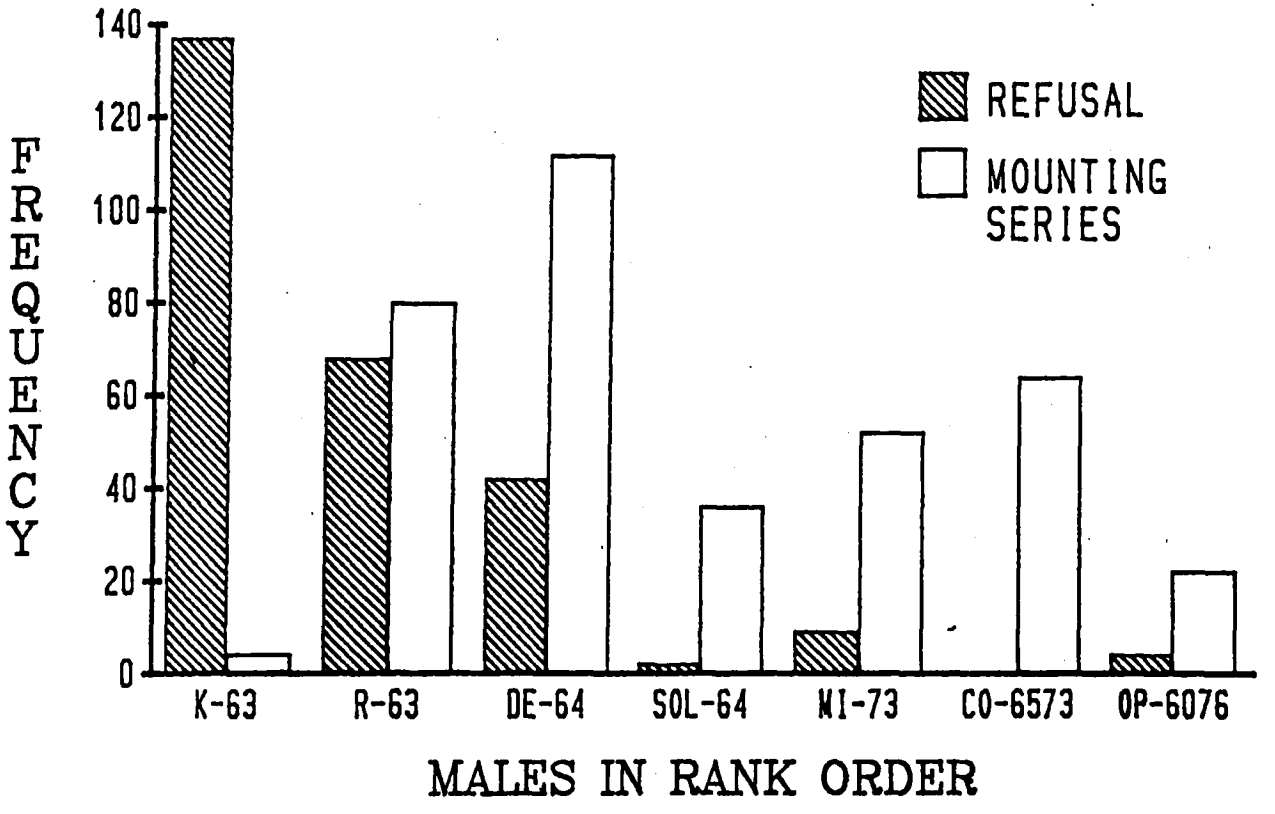
140
120
100
80
60
40
20
0
FREQUENCY
REFUSAL
MOUNTING SERIES
K-63
R-63
DE-64
SOL-64
MI-73
CO-6573
OP-6076
MALES IN RANK ORDER

Fig. 4